Some Aspects of the Feeding Behavior of *Remora remora*

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FOR SEVERAL YEARS the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, has been interested in holding captive tuna in ponds, and in 1958–59 conducted a series of tests of salt well-water as a medium for these fish. Preliminary experiments took place in a concrete cylinder 8 ft in internal diameter and 5 ft high, in which were confined a variety of reef and semipelagic fish, the latter being important because of our need to anticipate difficulties to be expected with the truly pelagic tunas.

Perhaps the most pelagic of these experimental fish was *Remora remora* (Linnaeus). Two specimens of this species were removed from tiger sharks, *Galeocerdo cuvieri* (Lesueur), on Jan. 16, 1959, and placed in the tank, which already contained several kinds of reef fish. The larger remora measured 170 mm in standard length, the smaller one 76 mm. The fish were fed every day, or every 2 days, and the remoras began eating bread on Jan. 23, continuing to take this and other foods throughout a 1-month observational period. The larger remora succumbed to an eroding infection of the head on Feb. 18, and the smaller one escaped through a drain on Feb. 23.

As soon as they were placed in the tank the remoras exhibited their characteristic attaching behavior. Both fish attached vertically with the head up, the larger fish in a small clearing in the algae coating the tank, the smaller fish to a concrete block placed on the tank's bottom. The larger fish continuously occupied its clearing for the month it lived, and during this period the algae encroached so that the clear space was the size and shape of the remora's disc. The smaller remora's habits were more variable, for it alternated between attaching to the concrete block, swimming freely at the surface, and attaching to the sides of black triggerfish (*Melichthys buniva* (Lacépède)) and parrotfish (*Scarus* sp.).

When first inducing the remoras to feed, food was dropped into the water as near as possible to them. It was soon discovered that they would detach to seize stray bits of food but would immediately reattach after eating, and the question then arose as to what competitive interaction existed between the attaching and feeding acts. A logical second question dealt with their sensory perception, for obviously they would not detach for undetected food. Another variable was the presence of other species, either the host which bore the remora or competitors for food. As these questions arose experiments were undertaken, and records were kept of the kind, quantity, and manner of presentation of food, as well as the behavior of the remoras and the other species. These records form the basis for the present report.

No unusual equipment or methods were employed, but the kinds of food should be listed. Bread was presented in the form of moistened compressed balls varying from ⅛ to ½ inch in diameter, depending on which remora was being fed. Fish consisted of freshly-killed tilapia (*Tilapia mossambica* (Peters)) and swordtails (*Xiphophorus helleri* Heckel) cut into transverse slices or cubes. Shrimp was offered in the form of small cubes cut from commercial frozen shrimp.

FEEDING VERSUS ATTACHING

Prior to examining the relative strength of the feeding and attaching urges in remoras it is necessary to say something about their sensory acuity toward food. Only the larger remora was observed for this, largely because of its single attached position. Food was offered to this animal from two directions: ventrally (toward the tank's center) or laterally (around the periphery of the tank). By starting with food presented

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close to the fish and progressing to offerings spaced increasingly distant it was found that the remora could detect food for at least 48 inches ventrally and 15 inches laterally. It is not known which sense was the most important in this detection, for the more distant offerings were tossed, striking the water with a splash which the fish undoubtedly heard. The water was clear, however, and this, together with the fact that *R. remora* normally feeds selectively on small zooplankters (Strasburg, 1959), may indicate that it could also see ¼-inch pieces of shrimp and bread.

The larger remora was increasingly reluctant to detach and feed when its food was offered from greater distances. Evidence for this is given in Figure 1, which shows the rapid decline in successful feedings with distance (excluding cases where food was approached by another fish). The longest feeding sally was 36 inches, although the fish made short ventures toward food dropped at 42 and 48 inches. The difference in behavior between ventral and lateral food presentations is not understood, but is possibly related to the concomitant binocular and monocular visual situations and the remora's relative ability to evaluate the distance to the food. Both eyes enter into the ventral profile and presumably provide the fish with binocular vision in this direction. All lateral food presentations were from such a direction that they could be seen only by the fish's left eye.

The extent of the larger remora's desire to attach is further manifested in its behavior when simultaneously confronted with two pieces of food. Food was presented ventrally in 25 double feedings at a distance from the remora of 1 to 15 inches. In 17 cases the fish detached, seized one piece of food, and dashed back to reattach to the tank wall, ignoring the second food fragment. In 6 trials the remora did this but immediately after reattaching sallied forth for the second piece of food. Once it ignored both foods and another time it ate both (at a distance of 8 inches) without attaching between feedings. For feedings involving three to eight pieces of food, behavior was much the same, the fish usually venturing out for a single particle, seizing it, returning to the tank wall to reattach, then venturing out again. Toward the end of its confinement it grew rather tame and would eat as many as five food fragments, without reattaching, if they were only a few inches from the attachment site. In general it would seem that the urge to attach is nearly as important as that to feed.

While attached to the concrete block on the tank's bottom, the smaller remora's behavior was much like the larger one's. It ventured after food offered at distances up to 14 inches and usually reattached immediately after seizing it. On three occasions this fish became temporarily free-swimming when food was presented, this occurring when numerous small food particles drifted close by. At such times the remora cruised back and forth through the showers of food at speeds of 0.2–0.4 ft per second, pursuing particles detected as far away as 24 inches. On four other days this fish was unattached throughout the observation period, swimming and feeding at the surface as described above.

The smaller remora spent a total of 11 days attached to triggerfish and 2 days to a parrotfish. The former hosts alternated between circling about the tank at 0.4–0.6 ft per second and wedging themselves into crevices between concrete blocks on the bottom. The remora did not feed when its hosts were in the wedged position. The parrotfish was demersal while it bore the remora, resting quietly on the bottom most of the time but occasionally dashing across the tank, rubbing its side against the bottom in an attempt to dislodge the remora. It appeared that the remora knew this host was a reluctant one, for it was unusually wary of becoming separated. On one occasion the remora had detached and was 2 inches from the parrotfish when the latter flexed its body; the remora, although within an inch of a piece of food, abandoned it to reattach to the host. Another time the remora had loosely attached to the parrotfish while masticating a large lump of bread. Its convulsive chewing and swallowing movements caused it to be displaced an inch or so from its attachment site. The remora's actions apparently disturbed the parrotfish, which tensed and shifted position each time the remora moved. This in turn affected the remora, which ceased chewing and clamped more tightly to the host each time it moved.

While attached to the triggerfish the small remora never ventured more than 6 inches in

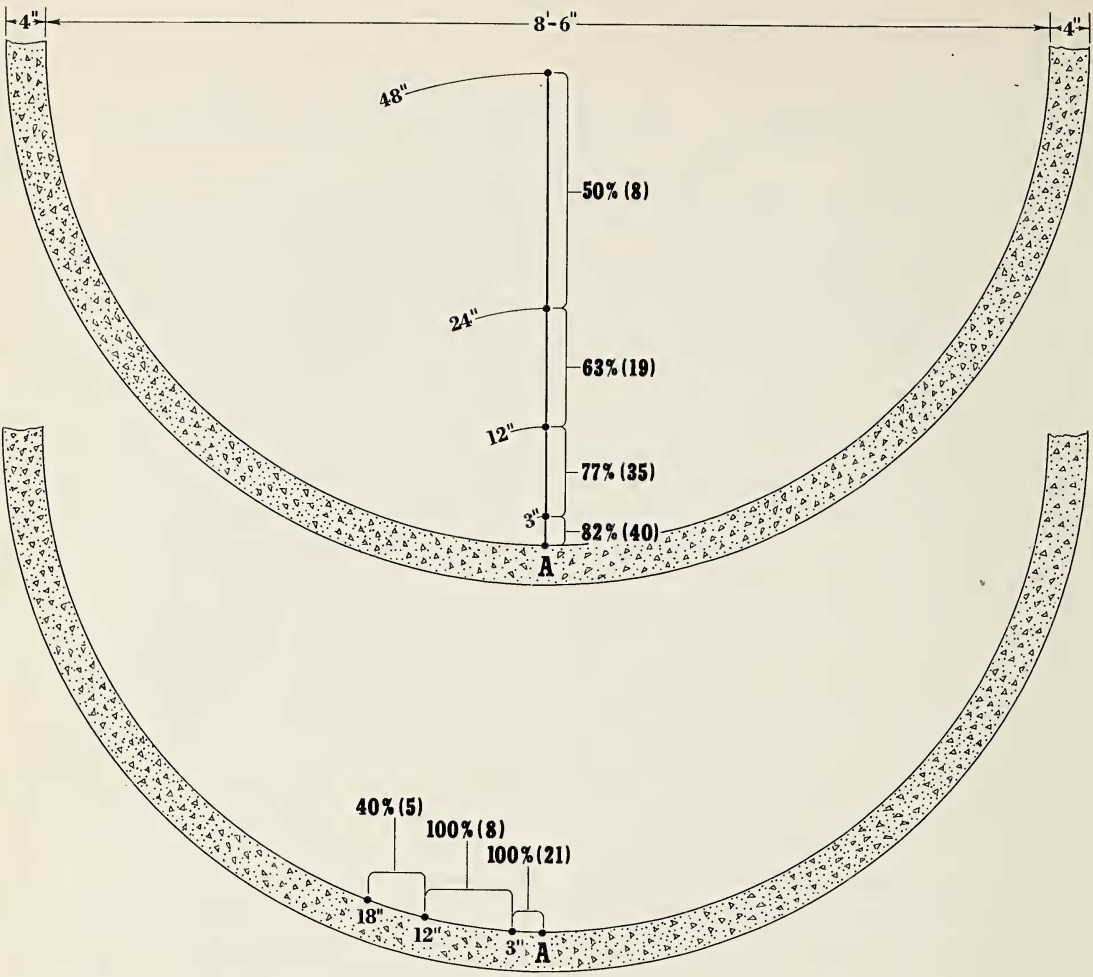

FIG. 1. Percentage occurrence of successful feedings when the larger remora was attached at point *A* and food was offered at successively greater distances. Figures in parentheses represent the total number of food presentations.

pursuit of food, although it reacted to food (by detaching and swimming a short distance) as far away as 12 inches. Of 44 food presentations made within 6 inches, 22 were culminated by the remora's making a successful feeding sally and 20 by an excursion part way to the food. All ventures were immediately followed by reattachment, and when large pieces of food had been seized, by leisurely mastication and swallowing. As noted above, the ingestion of food was often convulsive, resulting in a displacement of the remora by as much as 2 inches along the host's side. It appeared that large items could not be swallowed without loosening the grip on the host, while clamping more firmly to the host often meant losing food from the mouth.

Whenever a food particle fell near the host, the remora undertook a different type of movement in order to feed. The fish slid rapidly over the host's skin, moving forward, backward, or sideways with equal facility, and remaining so close to the host as to appear semi-attached. The extent of contact could not be determined, but probably the disk rim and the dorsal fin actually touched the host. These moves were used in going from the host's sides to the dorsal, anal, and caudal fins, and also in shifting from one side of the host to the other. Ten sliding movements were observed in detail: in six the

remora did not feed, its actions only allowing it to keep the food in view; twice the remora was able to seize food practically touching the host, and twice the remora first slid, then detached and swam to the food. This behavior again emphasizes the strength of the attaching urge in these fish.

RECOGNITION OF ATTACHMENT SITE

As noted earlier, the larger remora was a continuous occupant of a small clearing in the algae coating the tank wall. This was an oval space 3 inches high by 1 inch wide, located 11 inches beneath the surface. The surrounding alga was the diatom *Melosira,* which occurred as a dense growth up to 2 inches in thickness. The remora's disk fitted the clear space remarkably well, the disk being oval and 2¾ inches long by 1 inch wide. After each sally for food the remora returned directly to this site, centering its disk precisely in the clearing, and requiring no shifting of position because of misalignment. Its disk was never seen to overlap the clearing's edge nor were algal filaments ever seen to be drawn into the space beneath the disk. Despite the presence of numerous other alga-free spots in the tank, the larger remora restricted its attaching to this one.

A simple experiment was conducted to see whether this remora could be lured to a new attachment site. Two oval clearings were scraped in the algae, 6 and 12 inches to the left of the original site but identical in size and shape to it. Pieces of food were presented to the remora in such a way that it swam past the new clearings in order to feed. Many times the remora would seize its food within 2 inches of one of the new areas, but in no case could it be induced to attach in them.

The smaller remora was also able to recognize its precise point of attachment, at least when on its triggerfish host. This species, *Melichthys buniva,* is largely jet black in color, but when viewed in certain lights on some occasions it has a brilliant metallic green cast. When the remora detached from a triggerfish the skin to which it had been adhering was a much brighter green than the surrounding area, appearing as a horizontal oval spot on the host's side. When closely scrutinized, this spot was found to contain outlines of the disk laminae and rim, all visible as bright green marks against a black background. Each time the remora detached, it returned precisely to this spot, orienting itself to the spot's shape and position. Judging from preserved specimens, remoras have little or no dorsal vision, and it therefore seems that positioning is accomplished by some other sense. It is suggested that this is tactile and that the texture of soft attachment surfaces, such as a host's skin, becomes altered through long contact with the disk, enabling the remora to reestablish its position by touch.

EFFECT OF OTHER SPECIES

Among the factors affecting the feeding behavior of remoras are the presence of hosts, potential hosts, competitors, and predators. The host's role as a vehicle is obvious, and as such the rider is carried from place to place, provided with a respiratory flow of water (Strasburg, 1957), and furnished food in the form of ectoparasites (Strasburg, 1959) or scraps. These favorable characteristics are in part offset by the host's tendency to consume any remoras venturing near its mouth, and an inclination to dislodge or injure others by rubbing against hard objects. The beneficial aspects of the host outweigh the negative qualities, however, as is evidenced by a remora's conspicuous urge to attach.

The feeding experiments provided an opportunity to study the relation between an unattached remora and a potential host. This was done only for the smaller remora, because the larger one never attempted to attach to any of the relatively small hosts available to it. The smaller remora was free-swimming or attached to concrete blocks for 8 days following its capture. At this time two large triggerfish were added to the tank, and the remora attached to one or the other of these for the next 11 days, by which time both hosts had died. The next day the remora was attached to the next-largest available host, a parrotfish, the latter making vigorous efforts to rid itself of its adherent by scraping its sides against the bottom. The remora-parrotfish partnership was apparently mutually displeasing, for the remora left this host the same day, and during a 50-minute observation period was seen to make six passes at

other fish. Each pass consisted of the remora's swimming rapidly toward the other fish (*Acanthurus, Chaetodon,* and *Parupeneus*), increasing its speed as it went. The other fish allowed the remora to approach to about a foot, then made a violent turn and fled rapidly. While it is impossible to be certain, it is likely that these maneuvers were attempts to attach. After experiencing several such passes the other fish would no longer let the remora approach them, keeping about 18 inches away from it. This situation prevailed for the remainder of the period of captivity, during which the remora was only once successful in attaching to a fish. This occurred with the parrotfish and lasted for 1 day.

Although the smaller remora was bold when approaching another species, both remoras were very timorous when other species approached them. In 14 feeding experiments it happened that some other tank denizen was attracted to food meant for a remora. Usually the remora had detached and was part way to the food when it realized that another fish was approaching. This resulted in a rapid dash to the attachment site on the part of the remora, and a seizure of the food by the other species (*Parupeneus* and *Abudefduf*). On three occasions the two remoras competed with each other for food. Twice the larger remora abandoned the food to the smaller one, and once it waited until the smaller fish had passed the food before venturing toward it.

SATIATION

An incidental by-product of the feeding experiments was an estimate of the stomach capacity of the two remoras. Although most feedings were not conducted with this in mind, there were a few tests in which the fish were presented with known quantities of food until further offerings were ignored. Where the food was whole fish, volumes were ascertained by water displacement; where balls of bread or blocks of flesh were used, volumes were calculated on the assumption that the balls were spheres and the blocks cubes.

It was found that satiation in remoras resembled that in humans in that the fish not only had favorite foods but also tired of a particular item only to resume eating when a new course was offered. The larger remora became satiated with bread when it had consumed 0.4–2.0 cc; when fed bread until further offerings were ignored and then fed tilapia, satiety occurred with 4.1–4.3 cc; when fed tilapia alone the fish ceased feeding after eating 4.6 cc; and when given shrimp it ate 8.7 cc. A similar but less marked situation was found for the smaller remora. For it, satiety with bread occurred after eating 0.2–0.5 cc; for bread followed by tilapia it happened at 0.7 cc; for fish alone (*Xiphophorus*) it occurred at something less than 1 cc (consumption could not be completely witnessed); and for shrimp at 0.3 cc.

The volume of the 170 mm remora was 56 cc and of the 76 mm fish 4 cc. The largest meal eaten by each was 8.7 and 0.7 cc, respectively, giving a food volume per fish volume ratio of 16–17%. This seems to be typical for a regularly feeding predator, for Nakamura (Ms) found oceanic skipjack (*Katsuwonus pelamis*) consuming about 10% of their own weight at a single feeding, and Hatanaka et al. (1957) found mackerel (*Pneumatophorus japonicus*) consuming 12.5% of their own weight. If *R. remora* were dependent on scraps from its host, one would expect it to be able to ingest large meals and then forego feeding for some time. That it probably eats frequent small meals is suggested by its stomach capacity as well as by the observations of Strasburg (1959), who showed this species to subsist largely on zooplankters. These organisms are captured piecemeal and there is no need for ingesting a single large meal.

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